Species coexist more easily if reinforcement is based on habitat preferences than on species recognition

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Abstract: Maladaptive hybridization selects for prezygotic isolation, a process known as reinforcement. Reinforcement reduces gene flow and contributes to the final stage of speciation. Ecologically, however, coexistence of the incipient species is difficult if they initially use identical resources. Habitat segregation offers an alternative to species discrimination as a way to reduce gene flow: production of unfit hybrids is reduced if mate encounters become rare due to differing habitat choice. Using a modelling approach, we show that hybridization avoidance alone can select for habitat specialization, even if neither of the species is intrinsically better at using a specific niche. While habitat segregation and species discrimination both reduce the risk of producing unfit hybrids, these two isolation mechanisms differ from each other with respect to their effects on resource competition. Our model shows that, as a consequence of such differences, reinforcement evolves much more easily if hybridization is avoided based on habitat segregation than if the mechanism involves species recognition (mate choice traits). We also examine the outcomes when both isolation mechanisms evolve jointly. The establishment of one isolation mechanism a priori weakens selection for the other. However, an asymmetry persists here too. The net effect of habitat segregation on species discrimination was typically facilitative, but not vice versa. This asymmetry arises because habitat segregation, by enhancing coexistence, secures time for the subsequent evolution of species discrimination in a mate choice context (still relevant if habitat use is not perfectly segregated). Species discrimination does not have such a stabilizing effect on coexistence. Our results emphasize the importance of habitat segregation in reinforcement and offer a way to interpret findings where closely related taxa show similar performance on different resources or in different habitats. Studies of ecological generalization and specialization should therefore take into account that niche differences can be initiated and/or maintained by hybridization avoidance.

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Species coexist more easily if reinforcement is based on habitat preferences than on species recognition

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Summary

1. Maladaptive hybridization selects for prezygotic isolation, a process known as reinforcement. Reinforcement reduces gene flow and contributes to the final stage of speciation. Ecologically, however, coexistence of the incipient species is difficult if they initially use identical resources.

2. Habitat segregation offers an alternative to species discrimination as a way to reduce gene flow: production of unfit hybrids is reduced if mate encounters become rare due to differing habitat choice. Using a modelling approach, we show that hybridization avoidance alone can select for habitat specialization, even if neither of the species is intrinsically better at using a specific niche.

3. While habitat segregation and species discrimination both reduce the risk of producing unfit hybrids, these two isolation mechanisms differ from each other with respect to their effects on resource competition. Our model shows that, as a consequence of such differences, reinforcement evolves much more easily if hybridization is avoided based on habitat segregation than if the mechanism involves species recognition (mate choice traits).

4. We also examine the outcomes when both isolation mechanisms evolve jointly. The establishment of one isolation mechanism *a priori* weakens selection for the other. However, an asymmetry persists here too. The net effect of habitat segregation on species discrimination was typically facilitative, but not vice versa. This asymmetry arises because habitat segregation, by enhancing coexistence, secures time for the subsequent evolution of species discrimination in a mate choice context (still relevant if habitat use is not perfectly segregated). Species discrimination does not have such a stabilizing effect on coexistence.

5. Our results emphasize the importance of habitat segregation in reinforcement, and offer a way to interpret findings where closely related taxa show similar performance on different resources or in different habitats. Studies of ecological generalization and specialization should therefore take into account that niche differences can be initiated and/or maintained by hybridization avoidance.

Introduction

Reinforcement occurs when maladaptive heterospecific matings select for increased reproductive isolation between incipient species. The typical scenario involves allopatrically formed incipient species under secondary contact, where heterospecific matings are costly in terms of energy or other mating costs and/or low hybrid fitness (Servedio, 2001; Gröning & Hochkirch, 2008; Pfennig & Pfennig, 2009). This selects for increased prezygotic reproductive isolation, a process that contributes to the final stage of speciation (Servedio & Noor, 2003; Coyne & Orr, 2004).

Prezygotic isolation can become established by several alternative mechanisms, including behavioural and habitat isolation (Coyne & Orr, 2004). This raises the question of whether the mechanism behind reproductive isolation has an impact on the ease with which reinforcement evolves (Otto, Servedio, & Nuismer, 2008; Smadja & Bultin, 2011; Thibert-Plante & Gavrilets, 2013; Kopp et al., 2018). The majority of reinforcement theory concerns the evolution of species recognition (e.g., Liou & Price, 1994; Servedio & Kirkpatrick, 1997; Kirkpatrick & Servedio, 1999; Servedio, 2001), and habitat segregation has received much less attention (Coyne & Orr, 2004). Here, we

77 ask whether hybridization avoidance could select for habitat segregation, causing
78 ecological specialization that narrows the realized niche of species, even if the two
79 species in question do not differ in their intrinsic ability to use the niches on offer in the
80 environment. We also compare the ease with which reinforcement occurs if it is based
81 on habitat segregation with reinforcement that is based on species recognition (which
82 avoids hybridization without segregated habitat use), and ask what happens if both
83 mechanisms can operate simultaneously.

84

85 There are two good reasons (which are interrelated to one another) to address such
86 questions by modelling. The first reason relates to coexistence difficulties that arise
87 when two incipient species compete, presumably, for similar resources. Under an
88 assumption of sympatry, ecological competition may drive one or the other species
89 extinct even in the absence of hybridization (Sved, 1981; Templeton, 1981; Hubbell,
90 2001; Noriyuki, Osawa, & Nishida, 2012; Weber and Strauss, 2016). Our hypothesis is
91 that while habitat segregation and species recognition both offer ways to avoid
92 hybridization, they are not equally efficient in solving the problem of ecological
93 coexistence. Spatial conspecific aggregation, offered by habitat segregation, will lead to

94 more intense intraspecific than interspecific competition, stabilizing coexistence
95 (Chesson, 2000; Ruokolainen & Hanski, 2016). Incipient species can exhibit similar
96 ecological traits (Futuyma & Moreno, 1988; Wisheu, 1998; Friberg et al., 2015;
97 Noriyuki & Osawa, 2016; Rybinski et al., 2016), and in the absence of spatial
98 segregation they are predicted to experience intense ecological competition. According
99 to our hypothesis, hybridization avoidance might initiate and/or maintain spatial
100 segregation among closely related taxa, which is a very common pattern in nature
101 (Weber & Strauss, 2016).

102

103 Second, despite frequent reminders that habitat choice is a relatively easy path towards
104 assortative mating (Diehl & Bush, 1989; Johnson, Hoppensteadt, Smith, & Bush, 1996;
105 Gavrilets, 2004; Otto et al., 2008; Kopp et al., 2018), habitat isolation tends to be
106 interpreted as a by-product of local adaptation (Coyne & Orr, 2004). Most models
107 studying this phenomenon investigate whether local adaptation to different habitats can
108 create disruptive selection on habitat preferences and create conditions for sympatric
109 speciation, where hybrids are unfit because they are maladapted to both habitats (e.g.,
110 Felsenstein, 1981; Diehl & Bush, 1989; Johnson et al., 1996; Kawecki, 1996; Fry, 2003;

111 Gavrilets & Vose, 2005). Many models then investigate if behavioural isolation can also
112 evolve depending on the extent of ecological divergence (e.g., Felsenstein, 1981;
113 Johnson et al. 1996; Fry, 2003; Gavrilets, Vose, Barluenga, Salzburger, & Meyer, 2007).
114 The conceptual starting point of these models — variation in habitat characteristics —
115 leaves an important insight aside: habitat use may be influenced by reasons other than
116 efficient resource exploitation (Payne & Krakauer, 1997; Mills, 2005; Noriyuki, 2015;
117 Porter & Akcali, 2018; see also Mayhew, 2001). In sexually reproducing species, the
118 fitness of an individual may vary spatially due to variations in availabilities and
119 identities of potential mates, even if the intake of resources is equally efficient
120 everywhere. Therefore, habitat segregation can conceivably evolve to avoid
121 incompatible hybridization, without any difference in resource exploiting capabilities
122 (Noriyuki et al. 2012; Friberg, Leimar, & Wiklund, 2013; Noriyuki, 2015).
123
124 Explicit contrasts between habitat segregation and mate recognition as different routes
125 to reinforcement are rare. A notable exception is Yukilevich and True (2006), who
126 compared dispersal behaviour and mate choice in a secondary contact setting. In their
127 model that assumed an intrinsic postmating isolation mechanism (between two

128 populations with parapatric ranges), species recognition was more likely to evolve than
129 sedentary behaviour (which groups conspecifics) as a mean to avoid the production of
130 unfit hybrids. The difference was milder in their niche-based model variant that
131 introduces an aspect of local adaptation and thus favours movement patterns that avoid
132 crossing habitat boundaries. Even so, there remains a rather stark contrast between their
133 results and the general gist of sympatric speciation models, where habitat choice
134 appears to work very well to promote species divergence when compared with random
135 movement across habitats (Diehl & Bush, 1989; Fry, 2003).

136

137 Models of reinforcement involve either one-allele or two-allele mechanism; this
138 distinction relates to whether the cessation of gene flow requires the fixation of the same
139 allele between populations (e.g., if all females regardless of species identity prefer
140 males that match their phenotype, heterospecific matings will be rare), or whether
141 populations must differ in the alleles that fix (e.g., absolute preferences for a specific
142 phenotype of a mate). Yukilevich and True (2006) used a one-allele mechanism to
143 model the evolution of dispersal behaviour (i.e., sedentariness) and mate choice.
144 Obviously, these isolation mechanisms could also evolve via a two-allele model; the

two species could evolve preferences for specific habitats (Diehl & Bush, 1989; Kawecki, 1996, 1997; Fry, 2003; Berner & Thibert-Plante 2015, Nishida, Takakura, & Iwao, 2015), as well as divergent male signals and female mate preferences.

One- and two-allele models of dispersal behaviour can have qualitatively different characteristics. When sedentariness leads to local crowding and kin competition, sedentariness can be selected against for reasons that have little to do with hybridization (Fretwell & Lucas 1969; Hamilton & May 1977, Johnson & Gaines 1990). Migration modification in Yukilevich and True (2006) took the form of staying in the same habitat, and density dependence was implemented by sampling a fixed number of mating pairs to reproduce within each population. These authors do not explicitly discuss the implications of these choices for ecological competition. We adopt many features of the model by Yukilevich and True (2006) such as local density-dependence and no ecological differences between habitats, but adopt the two-allele assumption structure of other models to allow individuals to evolve preferences for specific habitats (e.g., host-plant segregation in phytophagous insects; Kawecki, 1996, 1997; Fry, 2003; Nishida et

al., 2015) and for specific signals. For a comprehensive comparison of previous and our models see Table 1.

We build three individual-based models that explicitly track population dynamics, gene frequencies, and gene flow. In the first two models, either species recognition or habitat preference, respectively, are responsible for the evolution of reinforcement (the 'species-recognition model' and the 'habitat-preference model'). Habitat serves as both mating and foraging site in our model, and thus mating and density regulation are habitat specific. Our third model allows the simultaneous evolution of both isolating mechanisms ('joint evolution model') to examine between-trait interactions (McPeek & Gavrilets, 2006; Yukilevich & True, 2006; Thibert-Plante & Gavrilets, 2013).

The model

Our individual-based model simulates secondary contact of two species (1 and 2), and begins with low initial population density for both species spreading into habitats A and B (e.g., two host plants) as a result of range expansion. The two species are identical in resource exploiting ability, and the resources offered by the two habitats are equal in

178 abundance and profitability. The habitats differ, however, in some feature (e.g., smell or
179 visual appearance) that allows for habitat preferences, should these evolve. Individuals
180 disperse (migrate) upon reaching reproductive maturity. Dispersers settle preferentially
181 in one type of habitat (A or B) should they have preferences for it. There is no other
182 spatial structure in the model. Mating and density regulation occur within each habitat.
183 Because resource competition is equally strong with conspecifics and heterospecifics,
184 there is no selection for habitat segregation in the absence of hybridization.
185
186 Both species are diploid and semelparous (generations are discrete). Individuals are
187 male or female. Organisms can evolve species recognition (male signal and female mate
188 preference) and/or habitat preference as premating isolation mechanisms. Each
189 individual has a locus M for a habitat preference, T for the male signal trait, P for
190 female mate preference, and D and E that are used to track species identity and the
191 production of hybrids. Some loci are only expressed in one sex as explained below;
192 additionally, some loci are not expressed in versions of the model where only one of the
193 two isolation mechanisms is allowed to operate. All loci are autosomal and recombine
194 freely; we assume they are initially in a stochastic Hardy-Weinberg equilibrium and

linkage equilibrium with each allelic value randomized independently, obeying an initial allelic frequency set for each species as described below.

The habitat-preference locus has alleles for preference for habitats A and B, and an allele for no habitat preference. The male signal-locus has alleles for two different attractive signals (e.g., vivid black and vivid white) and an allele for a signal that does not confer an attractiveness advantage (e.g., grey). The female mate-preference locus has alleles for preferences for each of the two attractive signals, and an allele for no mate preference. Regarding mate choice, we assume an open-ended preference function (i.e., stronger signals are more attractive, without there being a peak of optimal signal strength). If females prefer specific males, the less attractive males will suffer reduced fitness, which can drive species-recognition divergence due to sexual selection (Otto et al., 2008; Kopp et al., 2018).

The model incorporates three key parameters. We consider different values for the choice precision (α_{habitat} and α_{mate} for habitats and mates, respectively) that scales the likelihood that an individual with a preference achieves its desired outcome. A third

parameter, s_{hybrid}, specifies hybrid survival. Note that these parameters are set and fixed for a duration of one simulation run, not evolving; the model thus involves both evolving preferences (which alleles spread?) and fixed constraints (captured by 'precision') that limit the extent to which choosy individuals make choices that align with their preferences.

Each generation begins with dispersal. The habitat-preference locus M has three alternative alleles m_A, m_B and m_N, denoting preferences for habitats A or B or no preference, respectively. Allelic effects are additive. Let the probability of an individual with genotype x settling in habitat y be proportional to $\Psi_{habitat}(y|x)$ and given by $\Psi_{habitat}(y|x)/\Sigma_y \Psi_{habitat}(y|x)$. We assume $\Psi_{habitat}(A|m_Am_A) = \alpha_{habitat}$, $\Psi_{habitat}(B|m_Am_A) = 1$, $\Psi_{habitat}(A|m_Am_N) = (\alpha_{habitat} + 1)/2$, and $\Psi_{habitat}(B|m_Am_N) = 1$ ($\alpha_{habitat} \geq 1$). $\Psi_{habitat}(y|m_Bm_B)$ and $\Psi_{habitat}(y|m_Bm_N)$ are similarly defined. We assume that allelic effects of m_Am_B individuals cancel out, and thus $\Psi_{habitat}(A|m_Am_B) = \Psi_{habitat}(B|m_Am_B) = \Psi_{habitat}(A|m_Nm_N)$ $= \Psi_{habitat}(B|m_Nm_N) = 1$.

After dispersal, mating occurs within each habitat. Both male signal locus T and female mate-preference locus P show sex limited expression. T and P have alternative alleles (t_0, t_1, t_N) and (p_0, p_1, p_N), respectively. t_0 and t_1 produce different signals that are preferred by females with p_0 and p_1, respectively, whereas t_N induces no preferable signal and p_N induces no mate preference. Allelic effects are additive. Let the probability of a female with genotype x mating with a specific male individual with genotype y be proportional to $\Psi_{mate}(y|x)$. We assume $\Psi_{mate}(t_0t_0|p_0p_0) = \alpha_{mate}$, $\Psi_{mate}(t_0t_N|p_0p_0) = (\alpha_{mate} + 1)/2$, and $\Psi_{mate}(y|p_0p_0) = 1$ for $y \in \{t_1t_1, t_Nt_N, t_1t_N, t_0t_1\}$, and $\Psi_{mate}(t_0t_0|p_0p_N) = (\alpha_{mate} + 1)/2$, $\Psi_{mate}(t_0t_N|p_0p_N) = (\alpha_{mate}+3)/4$, and $\Psi_{mate}(y|p_0p_N) = 1$ for $y \in \{t_1t_1, t_Nt_N, t_1t_N, t_0t_1\}$ ($\alpha_{mate} \geq 1$). Preferences of p_1p_1 and p_1p_N females (i.e. $\Psi_{mate}(y|p_1p_1)$ and $\Psi_{mate}(y|p_1p_N)$) are analogously derived, while $\Psi_{mate}(y|p_Np_N) = \Psi_{mate}(y|p_0p_1) = 1$ for any y. Both females and males can mate multiply: females choose one mate for each of their young, with the probability that a specific male individual is chosen being proportional to his Ψ_{mate}.

Habitat preference, female mate preference and male signalling are all traits that are potentially costly to express. We assume that the cost is expressed as mortality during

habitat choice or mate acquisition. Females with (m_Nm_N or m_Am_B) × (p_Np_N or p_0p_1) genotypes and males with (m_Nm_N or m_Am_B) × (t_Nt_N or t_0t_1) genotypes all survive the dispersal and mate acquisition phases (mortality = 0). Strong habitat preference (m_Am_A or m_Bm_B) increases the individual's dispersal-mortality by $c_{habitat}$, and weak habitat preference (m_Am_N or m_Bm_N) increases it by $c_{habitat}/2$. Strong (p_0p_0 or p_1p_1) and weak (p_0p_N or p_1p_N) mate preferences increase the female's mortality during mate acquisition by c_{mate} and $c_{mate}/2$, respectively. Strong (t_0t_0 or t_1t_1) and weak (t_0t_N or t_1t_N) sexual attractiveness increases the male's mortality during mate acquisition by c_{signal} and $c_{signal}/2$, respectively. We keep the mortality increases moderate such that the sum of all effects never exceeds 1. In the simulation, we implemented these mortalities as occurring during dispersal, with additive effects (arguably a more realistic choice than multiplicative effects given that these are not sequentially occurring events but both occur at the same time).

After mating, each female produces $2R$ offspring, where R is the reproductive potential measured as the number of daughters. Offspring sex is assigned randomly. Offspring experience two rounds of mortality before dispersal. First, hybrids are selected against

262 due to genetic incompatibilities expressed at an early stage of life (e.g., before
263 hatching). To model species identity, we assume that the two diallelic loci D and E are
264 initially fixed for different alleles between species due to divergence during allopatry:
265 species 1 initially composed (d_1d_1, e_1e_1) individuals and species 2 (d_2d_2, e_2e_2)
266 individuals. Individuals with other genotypes are classified as hybrids; hybrids survive
267 with a probability s_{hybrid}.

268

269 Surviving offspring thereafter experience a second, density-dependent round of
270 mortality. We follow Liou and Price (1994) in assuming that the number of individuals
271 (male or female) surviving to the dispersal stage is $2NRK/[2RK + (R - 1)N]$ within each
272 habitat, where K is the carrying capacity measured in the number of females and N is
273 the number of individuals within the focal habitat immediately before density regulation
274 (Prout, 1978). In Prout's original formula, N it the number of reproducing mothers, and
275 replacing this with $N/2R$, which is the number of mothers that would have produced the
276 N juveniles in the absence of genetic incompatibility, leads to the above formula: note
277 that the original formula gives the number of daughters. The survivors of density

278 regulation are chosen randomly, and habitats A and B have identical values for R and K
279 unless otherwise mentioned.

280

281 Simulations begin with the adult stage (dispersal, followed by mating) of the first
282 generation. We initialize the populations by assigning allelic values with independent
283 draws from initial allelic frequencies. Frequencies of the three alternative alleles at M, T
284 and P are initially equal (except for stochastic deviation), unless otherwise mentioned.
285 Though equally frequent alternative alleles are arguably unrealistic, here we are
286 interested in the effects of selection and demographic dynamics, and thus we assume
287 maximum ancestral genetic variance. To simulate secondary contact during mutual
288 range expansion, we begin all simulations with low densities (100 individuals for each
289 species while $K = 1000$). Simulations are terminated if one of the two species becomes
290 extinct, if each species reaches near fixation for an allele at the habitat and/or mate
291 choice locus (in the joint evolution model, this criterion had to be reached by both loci),
292 or if the simulation had reached 20,000 generations. A locus was considered as nearly
293 fixed when an allele had an average frequency exceeding 95% measured over 100
294 consecutive generations (hereafter ‘fixation’). Outcomes with fixation were further

295 classified as “coexistence with an established reproductive isolation mechanism” if it
296 involved the fixation of different preference alleles (at M or P) between the two species.
297 Note that a fixation of the ‘no preference’ allele in either species does not qualify for
298 this criterion to be fulfilled. In the species recognition model, we used P rather than T to
299 define divergence, because T can fix for t_0 or t_1 solely through within-species sexual
300 selection in our model.

301

302 Simulations with the same parameter values were repeated for 100 times. Excluding
303 runs that led to extinction, the preference locus (loci) typically fixed (how an
304 exceptional run looks is shown in Figure S1).

305

306 **Results**

307 Most simulation runs result either in extinction of one of the species or coexistence with
308 reinforcement (illustrative examples are shown in Figure S2). Fusion of species is very
309 unlikely: we never observed fixation of a hybrid genotype, and hybrids were less
310 abundant than either parental species at the end of the simulation in > 99% of the runs.

311 We consequently report the proportion of runs that show two coexisting species with an
312 established isolation mechanism.

313

314 In the species-recognition model, coexistence with reinforcement is possible only when
315 mate choice is very precise, and even then coexistence is a rare outcome (Figure 1a).
316 This differs starkly from the habitat-preference model, where coexistence with
317 reinforcement is likely in a large part of parameter space (Figure 1b). These results are
318 robust to the introduction of a small fitness cost for expressing isolation traits (Figure
319 1cd). Relaxing the assumption of equal initial allele frequencies at the prezygotic
320 isolation loci affects the likelihood of coexistence with reinforcement in both isolation
321 mechanisms (Figure S3), corroborating previous findings on the importance of initial
322 allelic frequencies (Spencer, McArdle, & Lambert, 1986; Liou & Price 1994; Otto et al.,
323 2008).

324

325 We next examine the joint evolution of species recognition and habitat preference, by
326 assuming that individuals, if they have preferences, express the same precision of mate
327 and habitat choices ($\alpha_{habitat} = \alpha_{mate}$). The joint evolution model shows qualitatively

328 different results depending on the fitness cost of the isolation mechanisms. We first
329 report the results with cost-free trait expression. With three alternative alleles at all
330 prezygotic isolation loci (M, T, and P) being initially equally frequent, two species
331 manage to coexist when the choice is sufficiently precise and hybrid fitness is
332 sufficiently low (Figure 2ab). In almost all cases, coexistence is based on the joint
333 action of both isolation mechanisms (Figure 2e). Notably, species recognition evolves
334 much more commonly in this joint evolution model than in the species-recognition
335 model (Figure 1a vs. Figure 2a), i.e. allowing for the possibility of habitat choice greatly
336 facilitates the coexistence of two species, allowing for species recognition traits to also
337 evolve.

338

339 The joint evolution patterns are a result of a tug-of-war between one type of preference
340 facilitating or hindering the evolution of the other. On the one hand, one type of
341 preference may, by reducing hybridization, lessen the need to employ another. On the
342 other hand, we assume preferences to never be perfect: habitat preferences still allow
343 some migration between habitats, and species recognition likewise sometimes permits
344 hybrid matings. Too weak preference of either kind easily leads to the loss of one

345 species via demographic effects of hybridization and resource competition. Strong
346 preferences of one type can therefore, simply by aiding species coexistence, allow for a
347 hybridization situation to persist for long enough that the other type evolves.

348

349 However, there is an asymmetry here, because habitat preferences enhance coexistence
350 much more clearly than species recognition does. Simulations with different initial
351 allelic frequencies confirm that the results of Figure 2ab reflect a net facilitative effect
352 of habitat segregation on the subsequent evolution of species recognition. Assuming a
353 pre-existing preference for different habitats makes the evolution of species recognition
354 almost inevitable in a large part of parameter space (Figure 2c). This is because habitat
355 segregation stabilizes ecological coexistence by making intraspecific competition
356 stronger than interspecific competition through conspecific aggregation (Figure S4), yet
357 the remaining incompleteness of segregation selects for species discrimination through
358 the exchange of rare migrants.

359

360 On the other hand, allowing for the possibility of species recognition slightly lowers the
361 likelihood of coexistence with habitat segregation, when starting without a pre-existing

362 isolation mechanism (Figure 1b vs. Figure 2b). Another simulation shows that, in the
363 joint evolution model, pre-existing species recognition can either facilitate (if hybrid
364 fitness is high) or hinder (if it is low) the evolution of habitat segregation depending on
365 hybrid survival (Figure 2b vs. Figure 2d). These results are explained by additional
366 simulations that relax the assumption of $\alpha_{\text{habitat}} = \alpha_{\text{mate}}$ and show how pre-existing
367 species recognition affects the model behaviour (Figure S5). With no intrinsic
368 differences in species' ability to convert resources into offspring, pre-existing species
369 discrimination alone does not stabilize species coexistence (Figure S4). Demographic
370 stochasticity thus leads to unequal population sizes from initially equal abundances. For
371 the more common species, there is little reason to avoid using both habitats: this species
372 does not encounter heterospecifics that often, and mates with them even less often due
373 to the pre-existing species discrimination. The situation is reversed for the less common
374 species: it encounters many heterospecifics, and can be driven to extinction due to
375 frequent hybridization. Therefore, habitat segregation needs to evolve rapidly enough to
376 establish before the demographic asymmetry grows large. If pre-existing species
377 recognition is not very precise (Figure S5a), the model is similar to the habitat
378 preference model (Figure 1b). Increasing the precision of pre-existing species
379 discrimination reduces hybridization substantially to begin with, which weakens

reinforcing selection under low hybrid fitness and reduces genetic homogenization under high hybrid fitness (when hybrid fitness is high, gene flow is the major force countering the evolution of reproductive isolation; e.g., Figure 1). The net outcome is that hybrid fitness has little effect on the likelihood of habitat segregation evolving. Assuming sufficiently precise habitat choice, habitat segregation is now a moderately likely outcome across all values of hybrid fitness (Figures 2d and S5).

When isolation mechanisms are costly in the joint evolution model without a pre-existing isolation mechanism, coexistence with reinforcement in species recognition is restricted to a narrow range of intermediate choice precision and low hybrid fitness (Figure 3a). Simulations that independently vary the precision of both mate and habitat choice show that very precise mate choice prevents coexistence (Figure S6). Hybridization first selects for the divergence of both mate and habitat preferences (Figure S7), but as evolving choices progressively weaken selection for further divergence (which is opposed by the cost of the traits), habitat segregation remains incomplete. This creates conditions where stochastic demographic fluctuation and the resulting asymmetric hybridization risk, described above, lead to the decline and

397 eventual extinction of the less common species. Mate choice that is not too precise is
398 thus more favourable to coexistence, by maintaining selection for costly habitat
399 segregation. Meanwhile, very precisely expressed habitat choice is unfavourable to the
400 evolution of species discrimination (Figure S6), because it weakens the reinforcing
401 selection such that the evolution of costly species recognition is no longer necessary
402 (Figure S6). Intermediately precise habitat choice achieves sufficient spatial segregation
403 for coexistence combined with some exchange of migrants to maintain selection for
404 species recognition despite its costs. Therefore, the facilitative effect of pre-existing
405 habitat segregation on species recognition evolution is strongest at intermediate choice
406 precision values (Figures 3c and S6h).

407

408 Fitness costs of preferences likewise restrict the evolution of habitat segregation to
409 intermediate choice precision and low hybrid fitness (Figure 3b). The failure of habitat
410 segregation to evolve when choice is very precise was mainly due to the ecologically
411 destabilizing effect of the correlated very precise mate choice (as we assumed $\alpha_{habitat}$ =
412 α_{mate}), as discussed above (Figure S6). Despite all the complications described above,
413 the outcomes in the joint evolution model as a whole can be summarized as coexistence

414 with an established isolation mechanism being less easy to achieve in scenarios with
415 costly preferences (Figure 3) than in cost-free cases (Figure 2).

416

417 We have so far assumed that the quality (or size) of the habitats was identical, which
418 might have been favourable for habitat segregation. Versions of our model that relax this
419 assumption (by allowing habitat-specific fertilities and carrying capacities), however,
420 show qualitatively the same results (Figure S8 for models with one isolation
421 mechanism; Figure S9 for the joint evolution model). This shows that fitness costs of
422 hybridization can favour specialization, even onto a low-quality habitat.

423

424 **Discussion**

425 In our model, reinforcement based on just one mechanism evolves more easily if the
426 evolving trait impacts a habitat preference than if it impacts species recognition. Our
427 species recognition model is equivalent to a two-island model with 50% migration rate,
428 and thus rare reinforcement in this model is consistent with previous models (e.g., Liou
429 & Price 1994; Servedio & Kirkpatrick 1997; Yukilevich & True 2006). Remarkably,
430 however, habitat segregation frequently establishes in our model despite no initial

habitat use difference. Note that our model (unlike e.g., Kawecki, 1996, 1997; Fry, 2003) does not incorporate any mechanism to evolve better adaptation to a specific habitat, and in this sense the ability for habitat preferences to outperform species recognition (in the task of reinforcement-aided maintenance of two species) has been derived under conservative assumptions. Obviously, we do not wish to imply that real-world habitat preferences are *not* associated with local adaptation; we instead wish to highlight that managing hybridization risk alone can promote selection for two species to stay apart, which subsequently could also create conditions for specialization to utilize the habitats differentially.

In the joint evolution model (where both mechanisms are allowed to operate), the two isolation mechanisms show evolutionary interactions via their effects on coexistence and selection. These interactions are asymmetrical. While habitat segregation typically facilitates the subsequent evolution of species recognition, species discrimination instead suppresses the subsequent evolution of habitat segregation, except under limited circumstances. Habitat segregation renders populations primarily regulated by conspecific density, which promotes stable coexistence of the two species. During

448 prolonged coexistence, the few individuals that mistakenly settle in non-preferred
449 habitats maintain selection for species recognition.

450

451 This facilitative effect is absent in species recognition, which lacks the coexistence-
452 promoting effects described above. While species recognition reduces hybridization,
453 population abundances remain subject to stochastic fluctuations. Additionally, once one
454 species becomes substantially less abundant than the other, incomplete mate preferences
455 asymmetrically increase hybridization risk for the less common species, hastening their
456 extinction. Asymmetric abundance simultaneously weakens selection on the more
457 common species to specialize in the use of one habitat, which makes habitat segregation
458 difficult to evolve. When isolation traits were costly, 8.3% of simulation runs that
459 resulted in coexistence with reinforcement showed species discrimination but not
460 habitat segregation (Figure 3e). This result was obtained by terminating the simulation
461 runs upon fixation of both preference loci. Continued coexistence in later generations
462 would be difficult with prezygotic isolation based solely on species discrimination. The
463 results collectively suggest that reinforcement involving habitat isolation might be more
464 commonly found in nature than reinforcement involving behavioural isolation.

Our finding that habitat segregation to avoid hybridization can allow coexistence of otherwise ecologically identical species has implications for species coexistence (Chesson, 2000; Hubbell, 2001; Price & Kirkpatrick, 2009; Ruokolainen & Hanski, 2016). Closely related taxa, such as sister species, are often ecologically similar (e.g., Ohsaki & Sato, 1994; Veen et al., 2010; Friberg, Posledovich, & Wiklund, 2015; Sottas, Reif, Kuczynski, & Reifová, 2018), and simultaneously, habitat segregation is common among closely related taxa (Graves, & Gotelli, 1993; Cooper, Rodríguez, & Purvis, 2008; Cavender-Bares, Kozak, Fine, & Kembel, 2009). Although we do not aim to dismiss the role of local adaptation in producing habitat segregation, challenges remain: for example, host use by phytophagous insects is difficult to explain, because the quality of host plants as larval food shows poor correlation with adult oviposition preference (Futuyma & Moreno, 1988; Mayhew, 2001). If resource competition or physiological adaptation alone is unlikely to explain all patterns (e.g., Lawton & Strong 1981; Strong 1982), it is worth considering the causal role of heterospecific matings (reproductive interference, Noriyuki, 2015; Noriyuki & Osawa, 2016) in the evolution of habitat segregation.

Indeed, some empirical studies suggested that heterospecific courtship or mating have driven habitat segregation between closely related insect species (*Leptidea* butterflies: Friberg et al., 2013; *Harmonia* ladybirds: Noriyuki et al., 2012). Our results provide theoretical support for their claims, with additional emphasis on the synergistic effect of ecological similarity (see also Kishi & Nakazawa, 2013). On the other hand, an important open question is whether our assumption of habitat-specific density regulation (which we share with Yukilevich & True, 2006) is always appropriate. Most models (including ours) assume that densities are regulated at the same spatial scale as matings occur, but these could differ from each other for many reasons, e.g. individuals of some species travel to specific places to mate (e.g., see Colwell 1986).

Our model assumptions led to certain differences between our results and previous studies. First, in our model, fusion of species (persistent and frequent hybridization or the fixation of a hybrid genotype) was a rare outcome, unlike in the reinforcement model of Liou and Price (1994). These authors assumed independent density regulation for each species, with hybrids with intermediate genotype being randomly assigned either parental species identity. Under this assumption, when one species is rare, F1

499 hybrids that are assigned the identity of the less abundant species experience low
500 density-dependent mortality. This mechanism favours the hybrid genotype, because
501 hybrids, when divided into two populations with different species identities, potentially
502 enjoy relaxed population regulation. In our model, all individuals within a habitat
503 experienced density-dependent mortality with equal force, and hybrids experienced
504 additional (density-independent) mortality due to genetic incompatibility, hindering the
505 maintenance of a hybrid swarm.

506

507 Second, in our model, habitat specialization evolved despite the lack of differences in
508 habitat characteristics that would allow local adaptation. This scenario may not seem a
509 very conducive one for habitat preferences (although in Diehl & Bush, 1989, the
510 population splits into two even if the selection coefficient for local adaptation is set to 0,
511 this appears to be a consequence of the genetic architecture in their model not allowing
512 individuals to express zero preference). For example, theoretical work by Nishida et al.
513 (2015) has found habitat segregation to only evolve when hybridizing taxa exhibit a
514 trade-off in habitat specific fertility. In their model, fertility and density regulation were
515 both species specific. If interspecific competition is weaker than intraspecific

competition as assumed by Nishida et al. (e.g. foraging different parts of host plants), habitat occupied by one species can still be profitably exploited by the other. This selects against habitat specialization, which consequently requires more stringent conditions to evolve (e.g. trade-off in habitat-specific fertility). Equally strong intra- and interspecific competition removes such an effect. This explains why habitat segregation evolved relatively easily in our models.

Third, our findings of easier reinforcement by habitat segregation than by species recognition, and the facilitative effect of the former on the latter (but not vice versa), contrast with main findings of Yukilevich and True (2006; their intrinsic postmating isolation model). In addition to the difference in the genetic mechanisms (one- vs. two-allele), we made another different assumption: preferences in our model have finite precision. When organisms never make mistakes, the fixation of one isolation mechanism completely removes selection on the other, while in our model, hybridization risk can be reduced but never disappears entirely. This selects for the subsequent evolution of the other isolation mechanism, but only if the species are able to coexist ecologically. Indeed, a version of Yukilevich and True's (2006) model with

533 imperfect choice shows results that are more similar to ours (their Figure A3) than their
534 main results. In addition, Yukilevich and True's one-allele mechanism for habitat choice
535 made 'choosy' individuals simply stay in their natal habitat; in our model, individuals
536 who accidentally end up in the 'wrong' habitat will have offspring that are likely to
537 migrate back to where the habitat matches their preferences.

538

539 Other model assumptions of ours can also affect the outcome, warranting future work.
540 The precise way in which any isolation mechanism is implemented may impact our
541 findings (Berner & Thibert-Plante, 2015). Our two-allele formulation of both habitat
542 preferences and species recognition does not make them use the same number of loci.
543 Habitats can be chosen with a single locus, used by both males and females, whereas the
544 latter involves two (signal locus expressed by males, mate preference locus expressed
545 by females). The additional requirement of coevolution between two loci may
546 contribute to divergence based on species recognition being more difficult than that
547 based on habitat preferences — but this could also be seen to be a likely real feature that
548 distinguishes these two mechanisms. Notably, we in other respects made rather
549 favourable assumptions for species recognition to evolve (contrasting with the

550 conservative ones for habitat preferences, see above). We chose an open-ended mate
551 preference function, which can lead to mate preference divergence even without
552 hybridization (Otto et al., 2008; Kopp et al., 2018), and a male signal that exhibits no
553 environmentally determined variation. Environmental effects will ambiguate the
554 genotype-phenotype correlation of male signal and make reinforcing selection less
555 efficient.

556

557 Another avenue for further work is that the diversity of life histories is not fully covered
558 by our model. For example, in territorial birds, one could argue that the habitat is
559 typically first chosen by a male (via territory establishment), and then females can only
560 choose between 'packages' of both a territory and a male, with habitat and song and/or
561 plumage characteristics all playing a role. This would create a different set of sex-
562 specific assumptions than the choices we, or earlier modellers, have made. Lastly, we
563 used the default assumption of initially equal frequencies of all alleles at each
564 prezygotic isolation locus. Although it was an arbitrary choice to maximize genetic
565 variance, our choice is at least not unrealistic for habitat preference in the sense that it
566 leads to equal use of all habitats that should evolve in the absence of heterospecifics

567 (though this can also be achieved by the absence of any habitat preference). On the
568 other hand, species recognition traits might be unlikely to show high genetic variation in
569 allopatry especially with an open-ended mate preference function. Without
570 heterospecifics, our model reduces to the classical null model of sexual selection
571 (Lande, 1981; Kirkpatrick, 1982), where mate choice leads to the fixation of the
572 signalling trait , and thus the benefit of mate choice disappears.

573

574 To summarize, our results emphasize the importance of habitat segregation on
575 reproductive isolation and ecological coexistence between incipient species. Habitat
576 segregation has been well appreciated as an isolation mechanism both by theoreticians
577 and empiricists (Coyne & Orr 2004; Gavrilets, 2004; Kopp et al., 2018), but it has
578 typically been interpreted as a result of ecological adaptations to exploit different
579 resources. Intriguingly, closely related taxa often show similar performances on
580 different resources or in different habitats (Futuyma & Moreno, 1988; Wisheu, 1998;
581 Friberg et al., 2015; Noriyuki & Osawa, 2016; Rybinski et al., 2016). Our study shows
582 that habitat preferences can, at least in principle, be selected to diverge in the absence of
583 any trade-offs in resource use ability (local adaptation), which has implications for the

584 evolution of realized niches and the consequent number of species that can coexist in an
585 area (Hutchinson, 1957; Chase & Leibold, 2003; Lankau, 2011) in addition to the
586 speciation process itself.

587

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597

598 **Author contributions**

599 DK conceived the study, DK and HK designed the study, DK performed coding, and
600 DK and HK interpreted the results and wrote the manuscript.

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787 TABLE 1 Comparison between our models and related models.

Model	Framework	Spatial assumptions	Local adaptation	Prezygotic isolation mechanism(s)	One- or two-allele mechanism	Specific features
Felsenstein (1981)	Sympatric speciation	Two subpopulations, each with their own density regulation	+	Mate choice	2	Random dispersal (no habitat preference) despite local adaptation; single mating pool.
Diehl & Bush (1989)	Sympatric speciation	Two subpopulations, each with their own density regulation	+ (but neutral case also included)	Habitat choice	2	Matings are random either within each habitat or in a global mating pool (2 model variants).
Liou & Price (1994)	Secondary contact	One habitat, but implicit assumption that species use different resources	–	Mate choice	2	Disappearance of one species can happen via frequent hybridization, but not through being outcompeted ecologically, since density regulation operates independently in the two species.

Johnson et al. (1996)	Sympatric speciation	Two habitats	+	Habitat choice and mate choice	2	No habitat-independent reduction of hybrid fitness; if hybrids are unfit, this is due to local (mal)adaptation.
Kawecki (1996)	Sympatric speciation	Two habitats	+	Habitat choice	2	Beneficial mutations assumed to have habitat-specific effects.
Kawecki (1997)	Sympatric speciation	Two habitats	+	Habitat choice	1 and 2	Deleterious mutations assumed to have habitat-specific effects (harmful in one habitat only).
Fry (2003)	Sympatric speciation	Two habitats	+	Habitat choice	2	Speciation requires sufficient selection against residing in the wrong habitat; no other reason for hybrids to be unfit than local (mal)adaptation.
Gavrilets & Vose (2005)	Adaptive radiation	Many patches	+	Habitat choice	2	Many patches, many species; mating is random within a patch. Result: Local adaptation proceeds faster than habitat preferences that bring individuals to habitats where they are fit.

Model 1 (intrinsic isolation) of Yukilevich & True (2006)	Secondary contact	Two habitats, but no ecological differences (residing in one or the other is neutral, apart from mating interactions)	–	Habitat choice and/or mate choice	1	Hybrids are unfit without this relying on local adaptation. See main text for discussion of differences to our model.
Model 2 (niche-based) of Yukilevich & True (2006)	Secondary contact	Two habitats	Implicit (see rightmost column)	Habitat choice and/or mate choice	1	Conspecific ('homotypic') matings of the appropriate kind for this habitat yield fitter offspring than heterotypic or 'wrong' (for this habitat) homotypic matings.
Gavrilets et al. (2007)	Sympatric speciation	'Deep and shallow water'	+	Habitat choice and mate choice	2	Model designed to mimic a cichlid system; did not examine what happens if one mechanism operates alone.
Otto et al. (2008)	Assortative mating	Sympatry, potentially with grouping mechanisms	+	Habitat choice (impacting membership in groups) or mate choice	1	Model allows heterozygote fitness to be a frequency-dependent function of population-wide genotypic frequencies.

Berner & Thibert-Plante (2015)	Sympatric speciation	Original habitat, to which a novel habitat is added to be available for colonization	+	Habitat choice	1, 2, other	Comparison of four different habitat choice mechanisms.
Nishida et al. (2015)	Secondary contact	Many patches, each offering one of two host plant species	+	Habitat choice	2	Specialization (host partitioning) can occur as a result of reproductive interference, which reduces female fecundity if heterospecifics are present.
This study	Secondary contact	Two habitats, but no ecological differences (residing in one or the other is neutral, apart from mating interactions)	–	Habitat choice and/or mate choice	2	See main text for all assumptions and conclusions.

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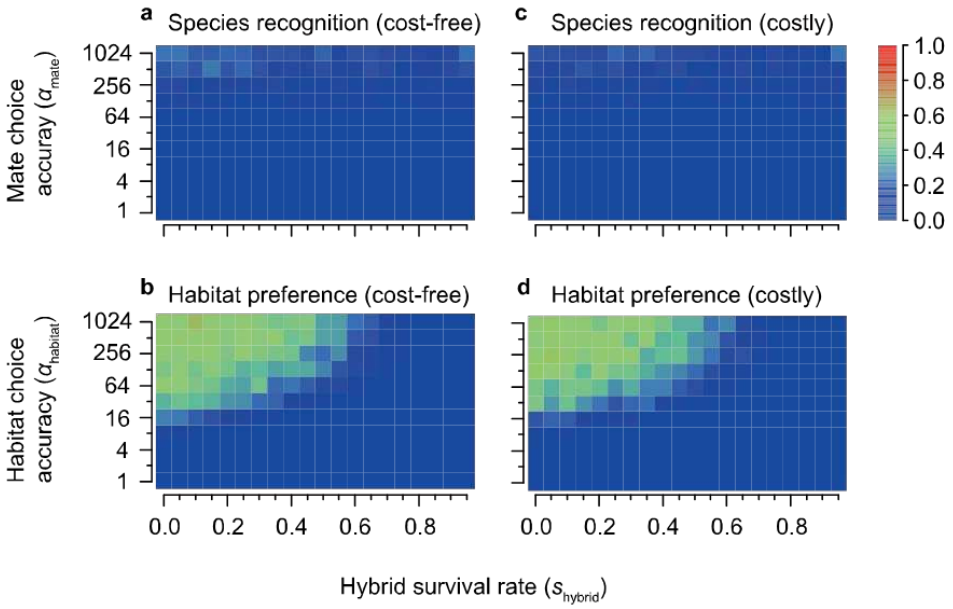
790

791 **Figure legends**

792 FIGURE 1



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794 Coexistence with reinforcement in models involving species recognition or habitat

795 preference, with or without costs of isolation mechanisms. Colours indicate the

796 proportion of simulation runs where two species coexisted and an isolation mechanism

797 became established (the alternative outcome was mostly extinction of a species). (a)

798 Cost-free species-recognition model; (b) Cost-free habitat-preference model; (c)

799 Species-recognition model with fitness cost; (d) Habitat-preference model with fitness

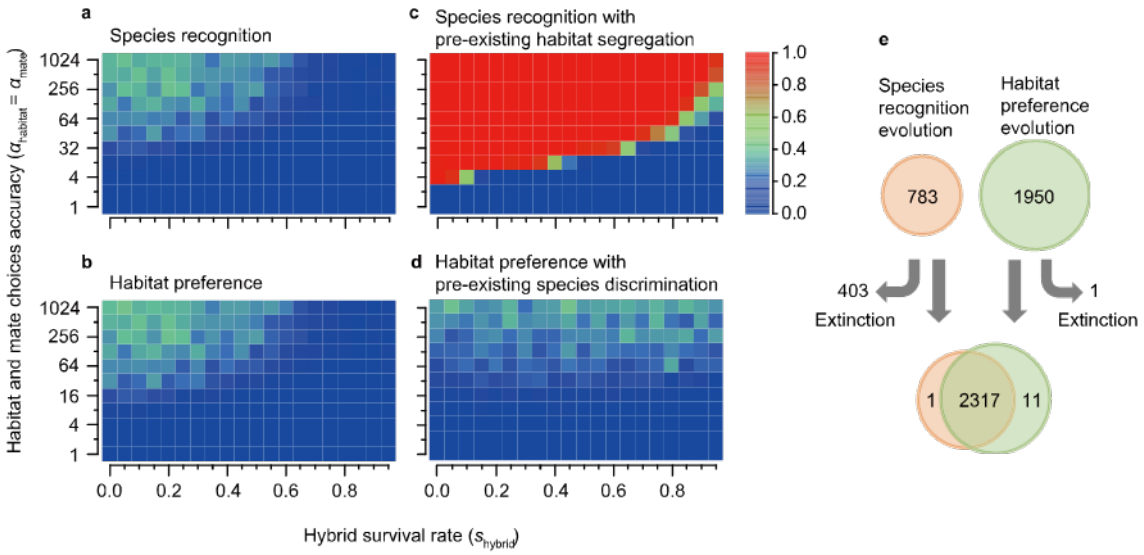
800 cost. Three alternative alleles at each prezygotic isolation locus (M, T, and P) were

801 initially equally frequent. Fitness costs of isolation traits were implemented as mortality

802 during dispersal ($c_{mate} = c_{habitat} = 0.01$, $c_{signal} = 0.02$). Initial abundance of each species

was 100 (male + female). Density regulation parameters were $R = 3.5$ and $K = 1000$. Simulation runs were replicated 100 times for each parameter combination.

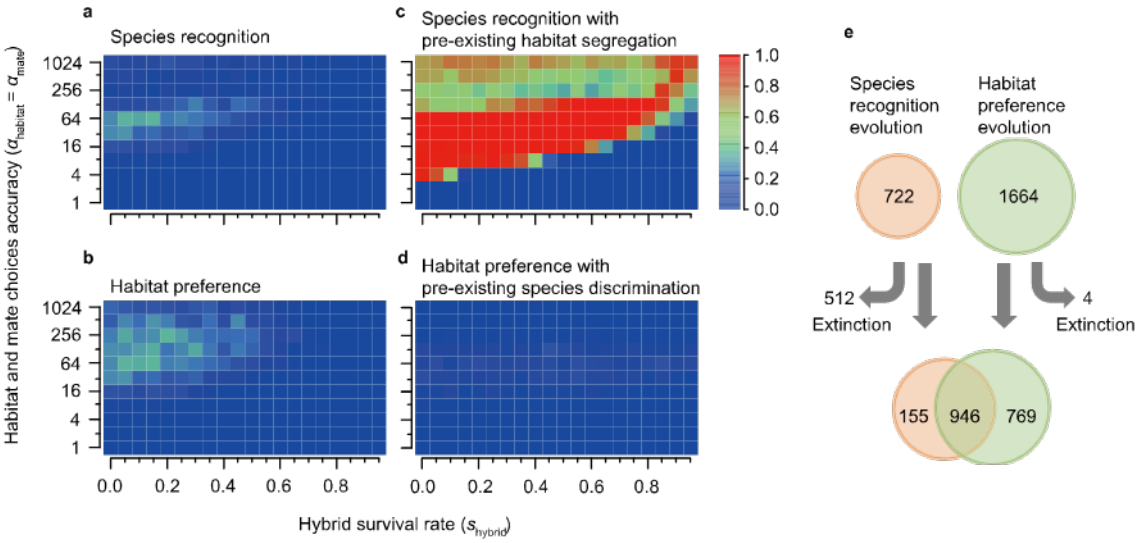
FIGURE 2



Coexistence with evolution of isolation mechanisms in the joint evolution model without fitness cost. Colours in (a), (b), (c) and (d) indicate the proportion of simulation runs where two species coexisted and an isolation mechanism (as indicated in the panel) evolved. Panels (a) (species recognition) and (b) (habitat preference) show the results from the same set of simulations, where all three alleles at prezygotic isolation loci were initially equally frequent. In (c), the two species were initially fixed for different habitat preference alleles, and in (d), the two species were initially fixed for different species

recognition alleles (male signals and female mate preferences). (e) Trajectories of isolation-mechanism evolution in runs underlying panels (a) and (b). A single isolation mechanism evolved in 2,733 out of 22,000 runs (species recognition was the first mechanism to evolve in 783 runs, habitat preference in 1,950 runs; in the remaining 19,267 runs, extinction but isolation mechanism evolution occurred), and in 2,317 of these runs this was followed by subsequent establishment of the second mechanism. Extinction of one of the species occurred in 404 runs after the evolution of an isolation mechanism. The species continuing to coexist based on one isolation mechanism only was a rare outcome (1+11 = 12 runs). Parameters (initial abundance, density regulation parameters, and replication effort) are as in Figure 1, with $c_{mate} = c_{habitat} = c_{signal} = 0$ (cost-free case).

FIGURE 3



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829 Coexistence with evolution of isolation mechanisms in the joint evolution model with

830 fitness cost. Colours in (a), (b), (c) and (d) indicate the proportion of simulation runs

831 where two species coexisted and an isolation mechanism evolved. Panels (a) (species

832 recognition) and (b) (habitat preference) show the results from the same set of

833 simulations, where initially all three alleles at prezygotic isolation loci were equally

834 frequent, while (c) shows outcomes when the two species were initially fixed for

835 different habitat preference alleles, and (d) shows outcomes when the two species were

836 initially fixed for different species recognition alleles (both in male signal and female

837 mate preference). (e) Trajectories of isolation-mechanism evolution in runs underlying

838 panels (a) and (b). A single isolation mechanism evolved in 2,386 runs (species

839 recognition was the first mechanism to evolve in 722 runs, habitat preference in 1,664

runs). Of these runs, 516 led to the extinction of one species, and joint establishment of both isolation mechanisms occurred in 946 runs. Fitness costs of isolation traits were implemented as mortality during dispersal ($c_{mate} = c_{habitat} = 0.01$, $c_{signal} = 0.02$). Initial abundance, density regulation parameters, and replication effort were as in Figure 1.